THE ORCHID EMBRYO SAC[1]

Lester W. Sharp

(WITH PLATES XXI–XXIII)

During the spring of 1910 it was the writer's privilege to visit the island of Jamaica as one of a party of botanists from the Johns Hopkins University under the leadership of Professor D. S. JOHNSON. In view of the number of orchids available in the region visited, it was suggested by Professor JOHNSON that a study of the embryo sacs of these species, together with those of certain forms growing in the University's greenhouse at Baltimore, might for several reasons prove of value.

The orchids, standing at the end of a great evolutionary line, the monocotyledons, and reaching extreme specialization in other features, may be expected to show instructive deviations from the usual type of embryo sac, and it is through a study of such deviations that a final explanation of the origin and nature of the angiosperm embryo sac will probably be reached. They should also be most likely to reveal the end result in the reduction of the female gametophyte, which is seen occurring as one passes from the lower heterosporous groups to the higher. Furthermore, the data at hand on the orchid embryo sac, in part very suggestive, have been somewhat scattered, the details being well known in comparatively few forms, so that we have not known just what relation the cases reported bear to any general situation which may be present among orchids.

Although the number of additional species here described is small for a group as large as the Orchidaceae, they are well scattered throughout the family, so that taken together with species previously described they place us in a better position to draw conclusions on the general tendency of the group.

For the sake of clearness the different forms will be considered separately, and only two or three of them in detail.

Epidendrum variegatum Hook.

The course of development in this species corresponds in many respects very closely to that recently reported for *Epipactis pubescens* (BROWN and SHARP 2), in which an 8-nucleate sac of the ordinary type is derived from one or less frequently from four megaspores. In *Epidendrum variegatum*, while the majority of sacs developed from one megaspore, the proportion of cases in which four are concerned is apparently greater than in *Epipactis*.

The archesporial cell, as in all of the other species examined, is hypodermal in position, and since it cuts off no parietals it is at the same time the megaspore mother cell. After passing through synapsis (fig. 1) and the other prophases preceding reduction, the nucleus of this cell divides. The position of the spindle and the wall formed upon its fibers is variable, which seems to be an important factor in determining the nature of the subsequent development. The spindle may be formed near the micropylar end of the mother cell, the resulting daughter cells in this case being very unequal in size, or the spindle may arise near the middle, the daughter cells then being approximately equal. Between these two positions of the spindle all gradations are found.

In the event of an unequal division the subsequent development is as follows. The small micropylar daughter cell at once begins to disorganize, while the large inner one divides (fig. 2) to form two megaspores. Of these the inner one only remains functional, the outer one disorganizing along with the micropylar daughter cell (fig. 3). The nucleus of the functioning megaspore divides without the formation of a wall (fig. 4) and the resulting nuclei again divide freely to form the 4-nucleate sac (fig. 5). At the next division (fig. 6) cell plates appear on the fibers of all four spindles, but those formed in connection with the chalazal nuclei usually disappear, so that the antipodals are in most cases represented by free nuclei.

When the division of the megaspore mother cell is equal (fig. 7), the cell plate which forms upon the spindle fibers is ephemeral and the two daughter nuclei are left free in the same cell cavity. Vacuolation occurs in the cytoplasm, usually in the region between the nuclei (fig. 8), but at times near the ends of the cell with the two nuclei at the center (fig. 9). At the division of these nuclei distinct

cell plates appear on the spindle fibers but do not persist, so that the four resulting nuclei remain free in the cytoplasm (figs. 10, 11). Since these have arisen by two successive divisions from the nucleus in which the heterotypic prophases occur, they are to be regarded as megaspore nuclei, and any one of them is thus the morphological equivalent of the nucleus shown in fig. 3. By one further division these four megaspore nuclei give rise to an 8-nucleate sac similar in all essential points to that derived from a single megaspore. An egg apparatus of the ordinary type is organized; the antipodal nuclei may or may not be separated by walls; and the two polar nuclei meet in the vicinity of the egg (fig. 12).

The various stages described in the foregoing paragraph may be distinguished from those in the development of a sac from a single megaspore by the absence of disorganized cells at the micropylar end. In later stages these latter become indistinguishable from the disorganized contents of the epidermal cells of the nucellus, so that it is then unsafe to use them as evidence, but there appears to be nothing against the assumption that the fate of the embryo sac is the same whether it has been derived from one megaspore or from four.

In this *Epidendrum*, as in *Epipactis*, two megaspores evidently take part in the formation of the embryo sac in a few cases. This condition results when the division of the megaspore mother cell is very unequal and that of the inner daughter cell equal, the separating wall at the second mitosis being ephemeral.

The pollen tube enters the sac, disorganizes the two synergids, and liberates two male nuclei. One of these fuses with the egg nucleus, while the other fuses with the two polars (fig. 13). The endosperm nucleus formed by the latter fusion undergoes no division, but degenerates along with the three antipodal nuclei (fig. 14).

The first few divisions of the fertilized egg are transverse, resulting in a filamentous proembryo of a varying number of cells. Longitudinal walls soon come in, and for a time the cells show a very regular two-ranked arrangement (fig. 15). Fig. 16 represents a proembryo of *E. verrucosum*, in which the number of transverse divisions has been very high, forming a filament of about 20 cells.

Figs. 17 and 18 show two stages in the development of the pro-embryo of *E. cochleatum*. In these three figures is seen the general course followed by the *Epidendrum* proembryo up to the stage found in the mature seed. Multiplication of cells commences at the chalazal end of the filament and extends upward, resulting in an oval mass of cells which is still to be regarded as a proembryo, since the body regions have not yet been marked out.

Epidendrum verrucosum Sw., E. cochleatum L., and E. globosum Jacq.

The embryo sacs of these forms were briefly examined. In the first two species stages were observed corresponding in all essential features to figs. 1, 3, 5, 12, and 14. In *E. globosum* were seen an ordinary 8-nucleate sac and a stage like that shown in fig. 14. It thus appears that *E. verrucosum*, *E. cochleatum*, and probably *E. globosum*, agree with *E. variegatum* in the formation of an embryo sac of the usual type from a single megaspore. The investigation of these three additional species was not carried far enough to determine whether they also show other methods of developing the embryo sac or not.

Phajus grandifolius Lour.

The early stages in the development of the embryo sac in this form correspond to those described above for those cases of *Epidendrum* in which but one megaspore is concerned in the formation of the sac.

The megaspore mother cell (fig. 19) divides unequally and the chalazal daughter cell again divides to form two megaspores. The outer daughter cell and megaspore disorganize (fig. 20), while the inner megaspore initiates the formation of the embryo sac. The nucleus of this functioning megaspore by two successive divisions gives rise to four; two of these lie at each end of the sac, the center of which is occupied by a large vacuole. The two chalazal nuclei undergo no further division, while those in the micropylar end divide to four (fig. 21), which become organized into an egg appa-ratus of the usual type and a free polar nucleus. This polar migrates toward the base of the sac and lies near the two chalazal

nuclei which have failed to divide (fig. 22). These three may fuse very soon (fig. 23) or they may remain distinct through the subsequent stages (fig. 24). In fig. 23 the egg apparatus fills an unusually large portion of the embryo sac.

The pollen tube discharges two male nuclei into the sac; one fuses with the egg nucleus and the other becomes associated with the free antipodal nuclei and micropylar polar (fig. 24). These latter nuclei show little regularity in behavior; they may begin to disorganize at any stage, but usually become more or less fused before this occurs. In any event no endosperm is formed.

The fertilized egg divides transversely to form a short filamentous proembryo, which attains a length of three or four cells before the first longitudinal division occurs. At this stage the cell toward the micropyle begins to elongate and push out into the surrounding placental tissue as a haustorial suspensor (figs. 25, 26). Later this dies away so that the proembryo in the mature seed is a simple rounded mass of cells (fig. 27).

Corallorhiza maculata Raf.

In *Corallorhiza* the embryo sac develops in a manner similar to that in *Phajus grandifolius*, as a comparison of figs. 28–33 (*Corallorhiza*) with figs. 20–24 (*Phajus*) will show. Consequently the above description of the sac of *Phajus* applies in all essential points to *Corallorhiza*, so that a separate account of the latter is unnecessary.

The proembryo of *Corallorhiza*, as described by LEAVITT (6), has a very long two-celled suspensor, which projects through the micropyle and enters the tissue of the placenta.

Broughtonia sanguinea R. Br.

This species shows the same peculiarity described above for *Phajus* and *Corallorhiza*. The innermost megaspore gives rise to a sac with six nuclei, the primary antipodal nucleus dividing only once. This division does not usually occur until the two nuclei in the micropylar end divide to four, so that three spindles are observed in the sac at one time.

Bletia Shepherdii Hook.

This form affords another example of the derivation of the female gametophyte either from one or from four megaspores, the course followed being apparently connected with the position of the wall formed at the division of the megaspore mother cell, as pointed out in *Epidendrum variegatum.* The nucleus of this cell goes into synapsis (fig. 34) and at its division the spindle may lie near the micropylar end of the cell or at its center. In the former case the daughter cells are very unequal in size; the small micropylar one degenerates, and the chalazal one divides to form two megaspores (fig. 35). Of these the outer one disorganizes, while the inner one enlarges and continues the development, by two successive divisions giving rise to the 4-nucleate embryo sac (figs. 36–38).

When the division of the megaspore mother cell nucleus occurs at the center of the cell (fig. 39) the wall formed is evanescent, the two nuclei thus being left free in the same cell cavity (fig. 40). These nuclei divide simultaneously, as shown in fig. 41; here the wall laid down at the first mitosis in the megaspore mother cell is still visible as a remnant, and several chromosomes are seen lying in the cytoplasm apart from the spindles. The four nuclei which thus arise, being the product of two successive divisions from the nucleus in which the heterotypic prophases occur, are to be regarded as megaspore nuclei (fig. 42).

Except for the absence of disorganized cells at the micropylar end, the 4-nucleate sac formed as just described is similar in appearance to that produced from a single megaspore (cf. figs. 38 and 42). Since the active growth of the sac results in the complete obliteration of the disorganized cells, it is not possible to determine by inspection of the later stages from which type of 4-nucleate sac they have been derived, but there seems to be no reason why either type or both should not continue the development, which from this point onward is exceedingly irregular. Abnormalities of many kinds were observed, and all that can be attempted here is to indicate one or two of the common tendencies shown.

In only three cases were there seen more than four nuclei in the embryo sac before fertilization. In one of these (fig. 43) the two micropylar nuclei had divided, resulting in a 6-nucleate sac like

that described above for *Phajus, Corallorhiza,* and *Broughtonia.*
In each of the other two cases the antipodal nuclei had also divided,
forming an 8-nucleate sac (fig. 44). In none of these sacs were
walls observed separating the nuclei at either end.

Since no walls are present at the 4-nucleate stage, the nuclei are
free to wander about through the sac (fig. 45). They were seen in
all positions, but sooner or later they may all fuse to form one
large nucleus. The most common course followed is that repre-
sented in figs. 46–48; the nuclei near each end of the sac fuse and
the resulting fusion nuclei do the same. Often all four fuse at once;
sometimes only two fuse; and in many cases degeneration sets in
before any fusions have occurred.

Apparently the pollen tube may enter the sac and discharge
its two male nuclei at any of these stages. In fig. 49 it has extended
to an unusual distance into a sac like that shown in fig. 47, and in
fig. 50 the male nuclei have been discharged into a sac containing
three nuclei in the central region. As far as could be determined,
no nucleus is set apart as the egg. The nuclei all lie in a group for
a time, and when disorganization does not occur at once they may
become fused (figs. 51–53). The large nucleus which results was
not observed to carry the development any farther.

In the material sectioned embryos proved to be exceedingly
scarce, and this condition is undoubtedly connected with the irregu-
larity and lack of organization shown by the embryo sac. The
two-celled proembryo in fig. 54 has evidently formed in a 6 or 8-
nucleate sac, as beside the pollen tube there are in the micropylar
end two disorganizing nuclei, probably synergids, and in the chalazal
region a partially fused and degenerating group made up of at
least three. The next few divisions in the proembryo are transverse
(fig. 55), so that in its early stages it is filamentous, as in *Epiden-
drum.* Meanwhile the placental tissue develops rapidly from all
sides, completely filling the cavity of the ovary, and the few pro-
embryos found were lying in the small intervening crevices.

It is not unlikely that the great irregularity shown by *Bletia* as
here reported may be due in part to the somewhat artificial con-
ditions under which the plant grew in the greenhouse.

Coelogyne massangeana and Pogonia macrophylla

In each of these forms the embryo sac contains eight nuclei derived in the usual manner from a single megaspore.

As is well known, the ovules of orchids do not develop far unless pollination has occurred. In most of the species here reported the pollen tubes are found growing among the ovules before the prophases of the reduction division in the megaspore mother cell; in one or two species they are not present before the embryo sacs reach the 2 or 4-nucleate stage. In reciprocal crosses between *Phajus grandifolius* and *Bletia Shepherdii* it was found that in both cases the pollen tubes develop in great numbers and grow down into the ovarial cavity, in which ovules develop and produce embryo sacs in smaller numbers but in the same manner as after normal pollination. In no case, however, was fertilization or an embryo seen resulting from crosses between these two species. Thus the stimulus necessary to the development of ovules with embryo sacs may be furnished by foreign pollen incapable of effecting fertilization.

Discussion

The main point of interest brought out in the above descriptions is the variability in development within the species. It has been noted by several workers that while the embryo sac of one species of a genus or family is formed from the megaspore mother cell directly, the sac of another species of the same group may arise from one of a row of megaspores. The same variation within the species has occasionally been observed, as in *Salix glaucophylla* (CHAMBERLAIN 4) and *Juglans cordiformis* (KARSTEN 5). In the Orchidaceae the latter condition appears to hold in a number of cases, the fate of the megaspore mother cell apparently being determined very largely by the position of the spindles at the first two divisions, as pointed out above for *Epidendrum variegatum* and *Bletia Shepherdii*, and recently for *Epipactis pubescens* (BROWN and SHARP 2).

This fluctuation results in a reduction in the number of divisions occurring between the megaspore and the egg. When a single

megaspore produces the 8-nucleate sac there are three such divi-
sions; when a similar sac arises from a daughter cell, two mega-
spores thus taking part in the process, there are two divisions; and
when the megaspore mother cell gives rise to the sac directly, four
megaspores are involved and the egg is separated from the mega-
spore by but one division.

The tendency to mature the egg earlier and earlier in the
ontogeny of the gametophyte is very conspicuous among gymno-
sperms, and it was hoped that among these very advanced angio-
sperms the end result of this specialization might be found—the
megaspore itself functioning as an egg. The number of cases in
which the elimination of but one more division would result in this
situation is fairly large, and includes sacs with 4 nuclei (*Cypri-
pedium*, PACE 7), 8 nuclei (*Lilium*, various orchids, and many
others), and 14 nuclei (*Pandanus*, CAMPBELL 3). That the reduced
condition is being approached by such a variety of ways allows us
to expect with confidence to discover in some plant a situation
exactly paralleling that in animals, in which the product of the
reduction divisions at once becomes the egg.

Scarcely less striking than the variability within the species is
the uniformity shown by the embryo sac throughout a group so
varied in structure and habit as the orchids.   In spite of the incon-
stancy in the methods of sac development the end result is remark-
ably uniform.   The ordinary 8-nucleate sac, developed from a single
megaspore, is the prevailing condition in the group.   Beside the
species here reported, it is found in *Calopogon* (PACE 8), *Habenaria*
(BROWN 1), *Epipactis* (BROWN and SHARP 2), *Gymnadenia* (WARD
10), *Orchis* (STRASBURGER 9), and others.

The influence of the surrounding conditions upon the behavior
of the nuclei during the formation of the embryo sac has recently
been considered in some detail (BROWN and SHARP 2).   The facts
brought out in the present account lend further support to the idea
there expressed, namely, that the causes for the behavior of the
nuclei are to be sought largely in factors external to the nuclei
themselves.   The conditions under which the ovules of orchids
develop within the ovary are undoubtedly much the same in the

various species, while the ovules themselves are almost exactly alike in structure, varying only in the matter of dimension. Thus since the archesporial cell in the different species has the same general form and initiates a series of stages developing under practically the same conditions, a general similarity in result is to be expected.

Whether a row of megaspores is produced or not seems, as already pointed out, to be largely dependent upon the position of the spindles at the first two divisions. But megaspore mother cell and functioning megaspore just before division are very much alike in size, shape, and surroundings, and are acted upon by similar external factors, so that whichever gives rise to the embryo sac the same course is followed and the same end is reached.

The 6-nucleate embryo sacs of *Phajus*, *Corallorhiza*, and *Broughtonia* seems to show a tendency toward a further reduction of the vegetative portion of the gametophyte.

In all of the species examined the endosperm nucleus, whether arising from the fusion of two or more nuclei, disorganizes without dividing, so that *Calopogon pulchellus* (PACE 8), in which it may give rise to as many as four free nuclei, remains as the only known case where endosperm is developed in orchids.

Summary and conclusions

1. The archesporial cell in all of the species examined is hypodermal and cuts off no parietals, thus becoming at once the megaspore mother cell.

2. The megaspore mother cell in all of the forms studied divides to two daughter cells, the chalazal one of which divides to form two megaspores. The innermost megaspore gives rise to the embryo sac.

3. In *Epidendrum variegatum* and *Bletia Shepherdii* the megaspore mother cell often gives rise directly to the embryo sac; in such cases four megaspores take part in the formation of the sac.

4. In *Epidendrum variegatum*, *E. cochleatum*, *E. verrucosum*, *E. globosum*, *Coelogyne massangeana*, and *Pogonia macrophylla* the embryo sac is of the ordinary 8-nucleate type. In *Bletia Shep-*

herdii the development is very irregular, but in fully mature sacs eight nuclei are present.

5. In *Phajus grandifolius, Corallorhiza maculata,* and *Broughtonia sanguinea* the primary antipodal nucleus divides only once, so that the embryo sac contains but six nuclei: four micropylar and two chalazal.

6. Polar fusion occurs in all of the forms studied. In the 8-nucleate sacs the fusion is between two equivalent polar nuclei. In the 6-nucleate sacs the micropylar polar migrates to the chalazal end and there fuses with the two nuclei which have resulted from the division of the primary antipodal nucleus.

7. In all of the species in which fertilization was observed it is of the usual type; one of the two male nuclei fuses with the egg nucleus, while the other fuses with the two polars.

8. The proembryo commonly consists of three cells before the first longitudinal division occurs; in *Epidendrum* a filament of as many as 20 cells may be formed. In the mature seed the body regions have not yet been marked out in the proembryo.

9. In all of the species examined the endosperm nucleus disorganizes without dividing.

10. The ordinary 8-nucleate embryo sac produced by a single megaspore is the prevailing condition among orchids. The causes for the comparative uniformity throughout the group are to be sought largely in the conditions surrounding the developing nuclei.

11. The orchids show very commonly a marked variation within the species. This variability, seen chiefly in connection with megaspore formation, is resulting in making an embryo sac in which the egg is removed from the megaspore by a single division a conspicuous feature in the group.

12. Although endosperm has been eliminated and the seed reduced to a very simple structure, the orchids as a group show in their female gametophytes very little advance over other plants, especially those lower in the line of the monocotyledons.

13. Reciprocal crosses between *Phajus grandifolius* and *Bletia Shepherdii* show that in these species the stimulus necessary to the development of ovules with embryo sacs may be furnished by foreign pollen incapable of effecting fertilization.

To Professor DUNCAN S. JOHNSON are due acknowledgments for many valuable suggestions during the progress of the work. The writer is also indebted to Mr. WILLIAM HARRIS for placing at his disposal material in the Hope and Castleton Botanic Gardens.

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EXPLANATION OF PLATES XXI–XXIII

All figures were drawn with the aid of an Abbé camera lucida, and show magnifications as follows: figs. 1–15, ×1200; figs. 16–18, ×295; figs. 19–24, ×1125; figs. 25, 26, ×513; fig. 27, ×295; figs. 28–33, ×1200; figs. 34–54, ×845; fig. 55, ×475.

PLATE XXI

Epidendrum variegatum Hook.

FIG. 1.—Synapsis in megaspore mother cell.

FIG. 2.—Inner daughter cell dividing; outer daughter cell disorganizing.

FIG. 3.—Functioning megaspore: outer daughter cell and megaspore disorganized.

FIG. 4.—Two-nucleate embryo sac: no wall on lingering spindle fibers.

Fig. 5.—Four-nucleate embryo sac.

Fig. 6.—Division to form eight nuclei.

Fig. 7.—Megaspore mother cell dividing equally; distinct wall formed.

Fig. 8.—Wall has disappeared; vacuole has formed.

Fig. 9.—Unusual arrangement of nuclei and vacuoles; nuclei in this case have gone into resting condition.

Fig. 10.—Division to form four nuclei; distinct cell plates formed.

Fig. 11.—Four-nucleate embryo sac (four megaspore nuclei): walls have disappeared.

Fig. 12.—Eight-nucleate embryo sac.

Fig. 13.—Double fertilization.

Fig. 14.—Young proembryo: endosperm nucleus and antipodals disorganized.

Fig. 15.—Proembryo.

Epidendrum verrucosum Sw.

Fig. 16.—Filamentous proembryo.

Epidendrum cochleatum L.

Figs. 17, 18.—Two stages of the proembryo.

PLATE XXII

Phajus grandifolius Lour.

Fig. 19.—Synapsis in megaspore mother cell.

Fig. 20.—Functioning megaspore: other daughter cell and megaspore disorganized.

Fig. 21.—Micropylar nuclei dividing; chalazal nuclei remaining undivided.

Fig. 22.—Six-nucleate embryo sac.

Fig. 23.—Same: egg apparatus formed; chalazal nuclei and micropylar polar fusing.

Fig. 24.—Fertilization: second male nucleus associating with other free nuclei of the sac.

Figs. 25, 26.—Proembryo showing micropylar cell growing out as a haustorium.

Fig. 27.—Proembryo from mature seed.

Corallorhiza maculata Raf.

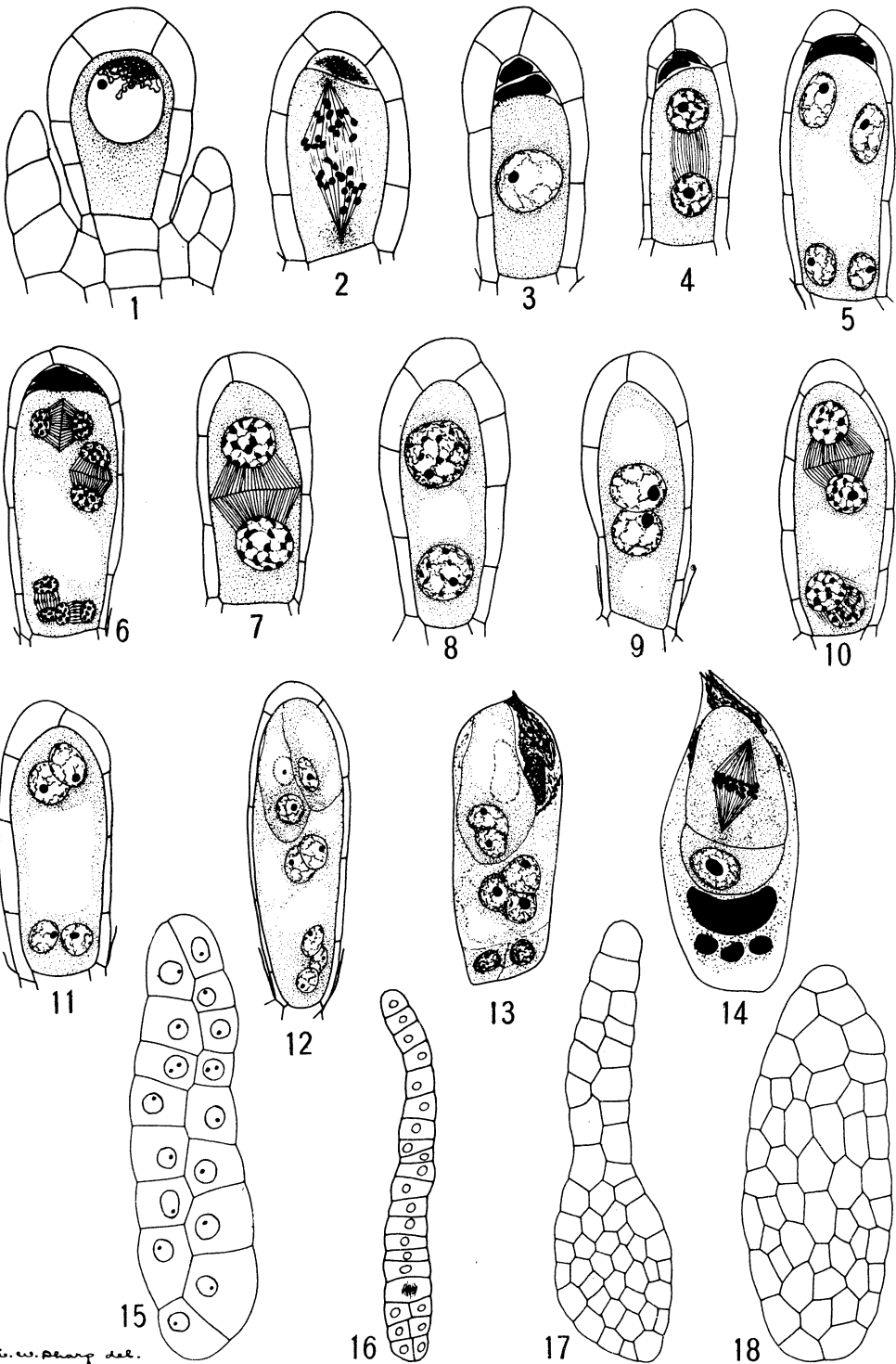Fig. 28.—Inner daughter cell of megaspore mother cell dividing; outer daughter cell disorganizing.

Fig. 29.—Four-nucleate embryo sac.

Fig. 30.—Micropylar nuclei dividing.

Fig. 31.—Six-nucleate embryo sac: micropylar polar has migrated to base of sac.
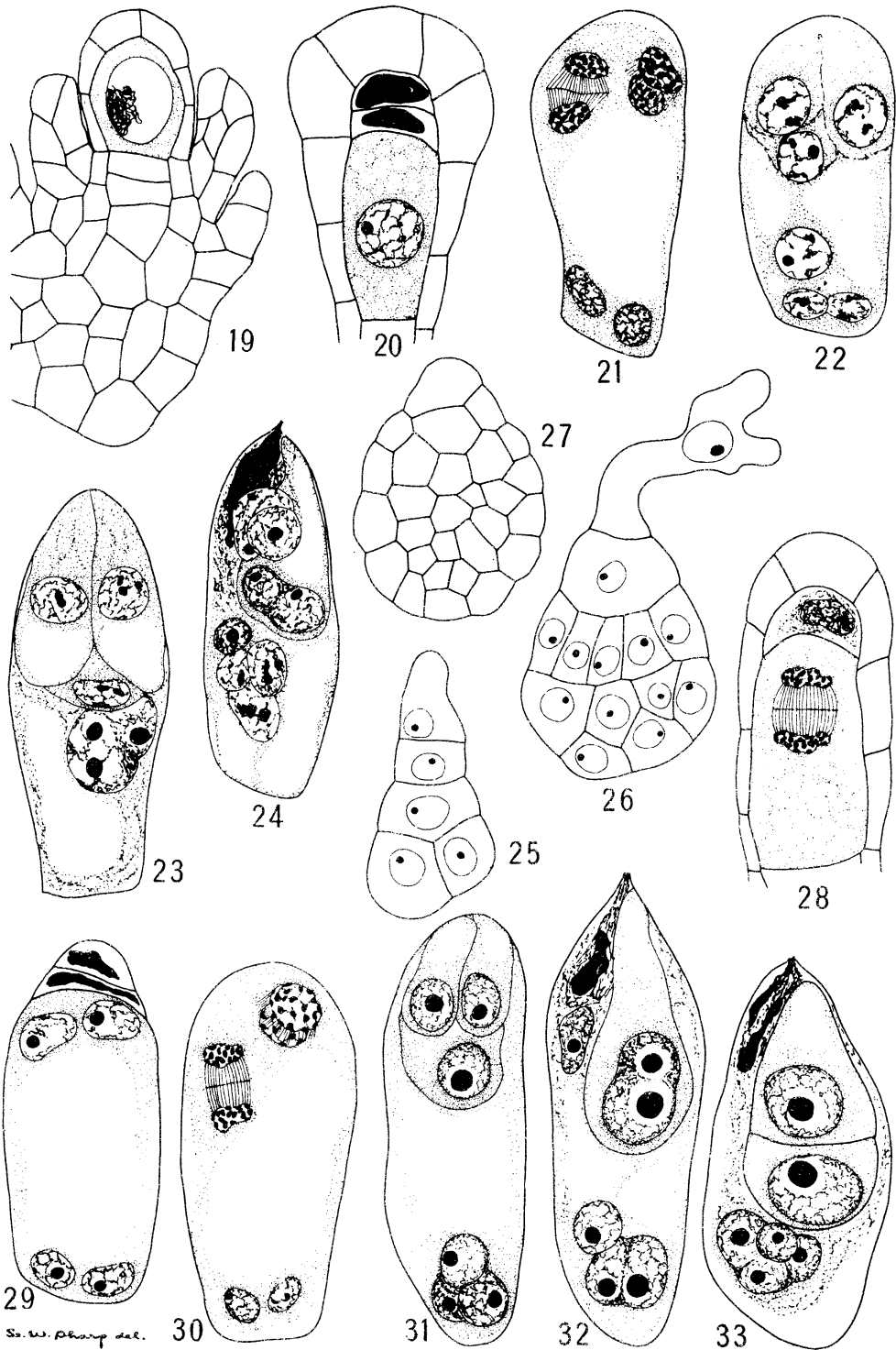
Fig. 32.—Fertilization has occurred; second male nucleus lying near egg.

Fig. 33.—Young proembryo: second male and other free nuclei of the sac fusing.
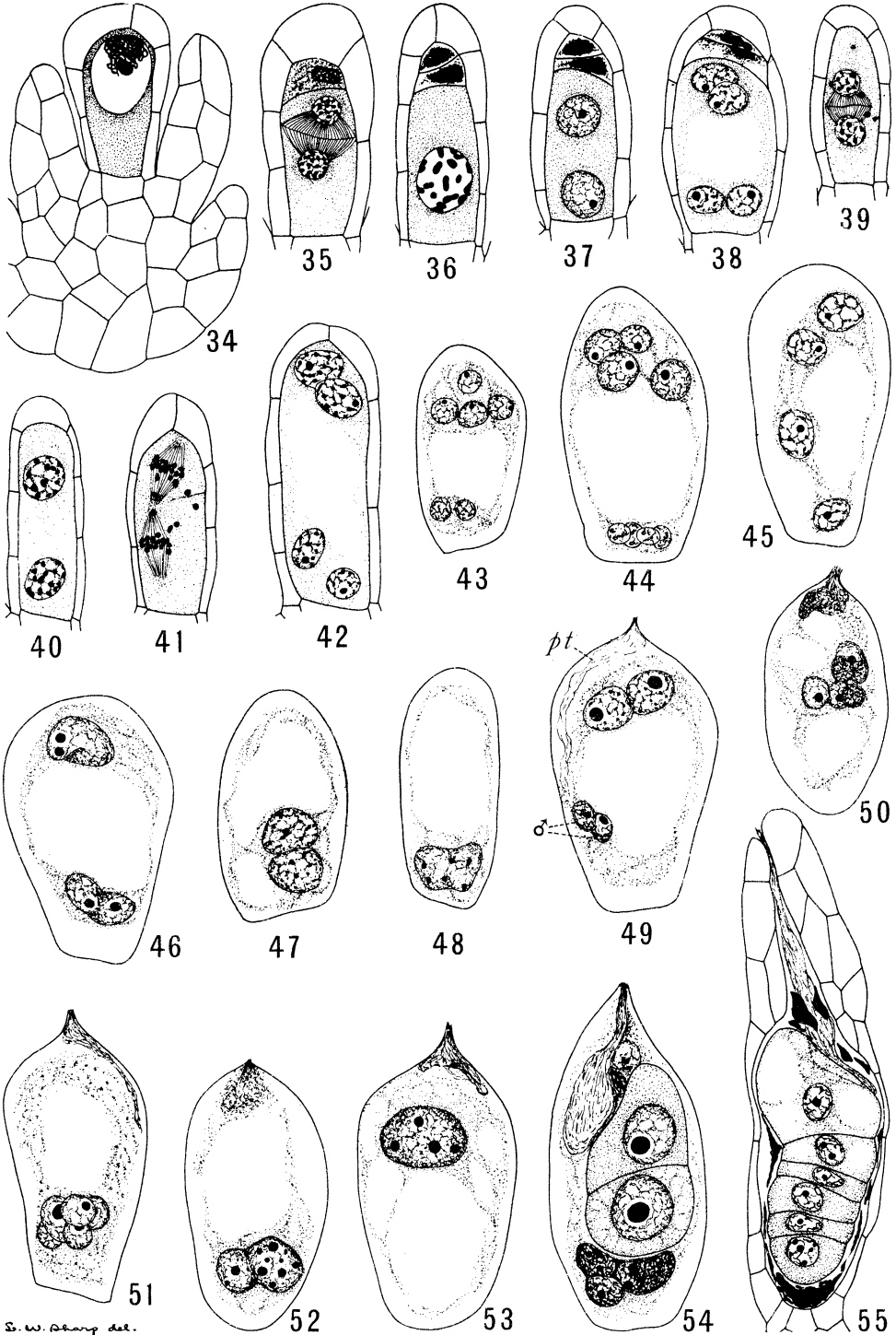
PLATE **XXI**

PLATE XXII

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SHARP on ORCHID EMBRYO SAC

PLATE XXIII

Bletia Shepherdii Hook.

FIG. 34.—Synapsis in megaspore mother cell.

FIG. 35.—Inner daughter cell dividing to form two megaspores.

FIG. 36.—Functioning megaspore: outer daughter cell and megaspore disorganized.

FIG. 37.—Two-nucleate embryo sac.

FIG. 38.—Four-nucleate embryo sac.

FIG. 39.—Megaspore mother cell dividing equally; wall forming.

FIG. 40.—Wall has disappeared.

FIG. 41.—Two nuclei dividing: wall formed at first mitosis still visible as a remnant in this case.

FIG. 42.—Four-nucleate embryo sac (four megaspore nuclei).

FIG. 43.—Six-nucleate embryo sac: micropylar nuclei have divided.

FIG. 44.—Eight-nucleate embryo sac: no separating walls.

FIG. 45–48.—Usual fate of the 4-nucleate embryo sac; all the nuclei fuse.

FIGS. 49–53.—Abnormal sacs into which male nuclei have been discharged; all the nuclei tend to fuse; *pt*, pollen tube; ♂, male nuclei.

FIG. 54.—Young proembryo evidently having formed in a normal sac.

FIG. 55.—Later stage of proembryo.